THE REPRODUCTIVE BIOLOGY OF *DIPLODUS SARGUS CAPENSIS* AND *D. CERVINUS HOTTENTOTUS* (SPARIDAE) OFF THE SOUTH-EAST CAPE COAST, SOUTH AFRICA

by

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ABSTRACT. - An investigation of the reproductive biology of *Diplodus sargus capensis* and *D. cervinus hottentotus* was undertaken in the Tsitsikamma National Park, South Africa. Gonado-somatic indices showed that both *Diplodus* species had protracted spawning seasons extending from early spring into summer. The adult sex ratio of *D. s. capensis* was significantly dominated by females while that of *D. c. hottentotus* showed no significant difference from a 1:1 sex ratio. Size at 50% maturity was calculated at 211 mm FL and 280 mm FL for *D. s. capensis* and *D. c. hottentotus* respectively. This corresponded to an age of three and six years respectively. A detailed histological examination of gonad development revealed that *D. s. capensis* is a digynous hermaphrodite with partial protandry occurring in some of the male population. *D. c. hottentotus* is shown to be a rudimentary hermaphrodite. Group spawning behaviour in both species is postulated, based on various morphological and indirect behavioural characteristics.

RÉSUMÉ. - Biologie reproductive de *Diplodus sargus capensis* et *D. cervinus hottentotus* (Sparidae) sur la côte sud-est du Cap, Afrique du Sud.

Des recherches ont été entreprises sur la reproduction de *Diplodus sargus capensis* et *D. cervinus hottentotus* dans le parc national de Tsitsikamma, Afrique du Sud. Les indices gonado-somatiques ont montré que les deux espèces ont des saisons de ponte qui s'étendent du début du printemps jusqu'à l'été. La sex-ratio de *D. s. capensis* est significativement dominée par les femelles tandis que celle de *D. c. hottentotus* ne présente pas de différence significative par rapport à 1. La taille à la maturité sexuelle 50% est de 211 mm et de 280 mm (longueur à la fourche) pour *D. s. capensis* et *D. c. hottentotus* respectivement. Cela correspond à un âge de 3 et 6 ans respectivement. Un examen détaillé du développement des gonades a révélé que *D. s. capensis* est un hermaphrodite avec une protandrie partielle qui a été observée dans quelques populations de mâles. *D. c. hottentotus* est un hermaphrodite rudimentaire. Les deux espèces auraient un comportement de ponte en groupe, une hypothèse fondée sur des caractéristiques comportementales et morphologiques variées.

Key-words. - Sparidae, *Diplodus sargus capensis*, *D. cervinus hottentotus*, PSW, South Africa, Reproduction, Sex change, Hermaphroditism.

Sparid fishes exhibit a diverse sexuality (Atz, 1964; Reinboth, 1970; Thresher, 1984) which may be expressed as either sequential hermaphroditism (protandry or protogyny) or "late" gonochorism (rudimentary hermaphroditism) (Buxton and Garratt, 1990). The expression of this sexuality is complex in many sparid species and its interpretation rather difficult (Matsuyama *et al.*, 1988). Nevertheless, interpretation of this sexuality is an important factor in understanding the reproductive style exhibited.

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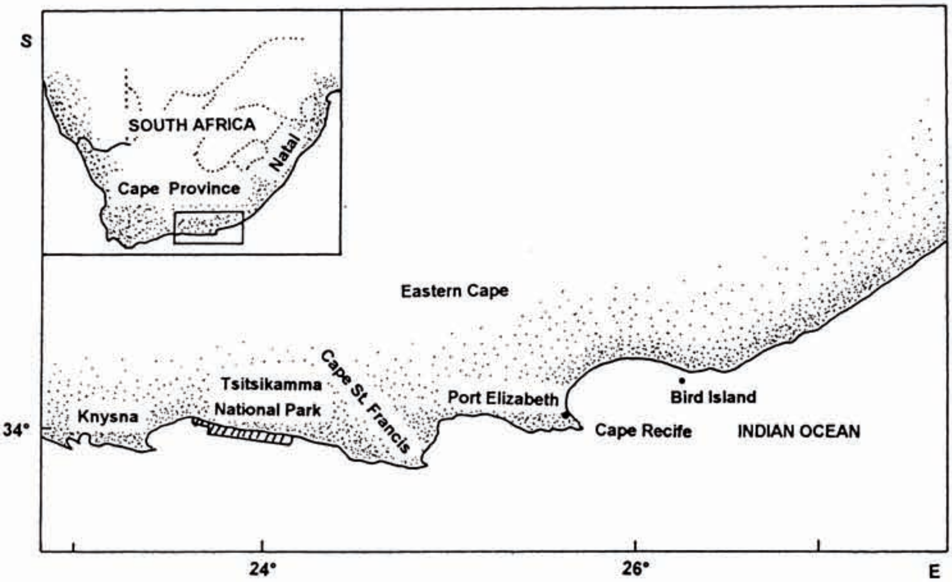


Fig. 1. - Position of the Tsitsikamma National Park on the south-eastern Cape coast, South Africa.

Reproductive studies done in South Africa on several important recreational and commercial sparid linefish have shown that the majority of these species are either protogynous or rudimentary hermaphrodites (Mehl, 1973; Hecht and Baird, 1977; Coetzee, 1983; Garratt, 1985; Pulfrich and Griffiths, 1988; Smale, 1988; Buxton, 1990; Garratt, 1991; Buxton and Clarke, 1991, 1992; Bennett, 1993), although there have been some reports of protandry (Lucks, 1970; Coetzee, 1986; Garratt, 1993).

Previous research on the reproductive biology of *Diplodus* species in South Africa has focused on *D. sargus capensis* (Joubert, 1981; Coetzee, 1986) but confusion surrounds the type of hermaphroditism exhibited by this species. It has been described as both a rudimentary hermaphrodite (Joubert, 1981) and a protandrous hermaphrodite exhibiting a special form of protandry (Coetzee, 1986). Studies done on *D. sargus sargus* in the Mediterranean and *D. sargus kotschyi* in the Persian Gulf have described these subspecies as protandrous (Micale *et al.*, 1987; Abou-seedo *et al.*, 1990; Micale and Perdichizzi, 1994) although rudimentary, non-functional hermaphrodites of the same subspecies have also been described (Reinboth, 1962; Lissia-Frau, 1968). Very little work has been done on the sexuality of *D. cervinus hottentotus*, although the spawning seasons of both species have been described (Christensen, 1978; Brownell, 1979; Beckley, 1985). By definition, protandrous hermaphrodites function first as males after which they change sex and function as females, with all females necessarily being derived from males (Buxton and Garratt, 1990). Rudimentary hermaphrodites are where males and females develop from an immature bisexual gonad prior to sexual maturation and no sex change occurs in mature individuals.

To gain an insight into the reproductive style exhibited by both species, various aspects of their reproductive biology were investigated. These included determination of reproductive seasonality, length frequency distribution of sexes, sex ratios and size/age at sexual maturity. In addition to this, a detailed histological examination of gonad development in both species was undertaken as this is an indispensible pre-requisite for the diagnosis of hermaphroditism (Reinboth, 1970).

MATERIAL AND METHODS

Monthly samples of *D. s. capensis* and *D. c. hottentotus* from all size classes were collected by spearfishing and linefishing in the Tsitsikamma National Park (TNP) and adjacent areas between April 1989 and December 1990 (Fig. 1). The 382 *D. s. capensis* and 304 *D. c. hottentotus* sampled were weighed (grammes), measured (millimeters fork length) and sexed macroscopically. Gonads were then dissected from the fish, weighed and visually assessed for their stage of maturation according to the criteria in table I (Buxton, 1990). Macroscopic staging of gonads was later verified by histological examination.

To investigate the seasonality of spawning, a monthly gonado-somatic index (GSI) was calculated as a percentage for individual fish:

$$GSI = \frac{\text{Gonad mass (g)}}{\text{Eviscerated body mass (g)}} \times 100$$

For histological examination, sub-samples of gonadal tissues were fixed in Bouin's solution for three days and then stored in 60% propyl alcohol. They were then embedded in paraffin wax, sectioned at 7 µm and stained using Gill's haematoxylin, OG 6 and EA 65 cytoplasmic stains. Sections were examined using light microscopy.

Sadovy and Shapiro (1987) recommend that in order to infer protandry the following steps be taken: i) to hypothesize a sequence of development based on regular differences in gonadal histology of successive sizes; ii) to show evidence of intermediate individuals containing degenerating spermatogenic and developing ovarian tissue; iii) to induce sex change experimentally. Experimental induction of sex change was beyond the scope of this study but, in an attempt to resolve the type of hermaphroditism exhibited by *D. s. capensis*, the first two recommendations were incorporated into this study.

RESULTS

Reproductive seasonality

In *D. s. capensis*, monthly gonado-somatic indices showed an extended spawning season, peaking in spring (August to October), but with relatively high GSI values being recorded throughout summer until March (Fig. 2). This extended spawning season, coupled with histological evidence of ripe ovaries containing oocytes in various stages of maturation, suggest that oocyte development is asynchronous (Garratt, 1985) and that *D. s. capensis* is capable of multiple spawnings per spawning season (Wallace and Selman,

Table I. - Description of the macroscopic maturity stages in *Diplodus sargus capensis* and *D. cervinus hottentotus* (from Buxton, 1990).

1. Inactive/resting	Gonads small. Testes thin and transparent to off-white in colour. Ovaries long and thin, translucent orange in colour.
2. Developing	Gonads increase in size. Testes show some thickening and are white in colour. Sperm is visible if the testes are cut and gently squeezed. Ovaries become swollen and orange/yellow in colour. Eggs are visible to the naked eye.
3. Ripe	Testes very large and swollen. They are white in colour but often become pinkish as the breeding season progresses. Sperm is found in the testicular tissue and the main sperm duct. Ovaries very large and yellow in colour. Translucent eggs are visible in the tissue and in the lumen.
4. Spent	Testes decreased in size and pinkish-grey in colour. Sperm may still be present in the main sperm duct. Ovaries are flaccid, bloodshot and reduced in size.

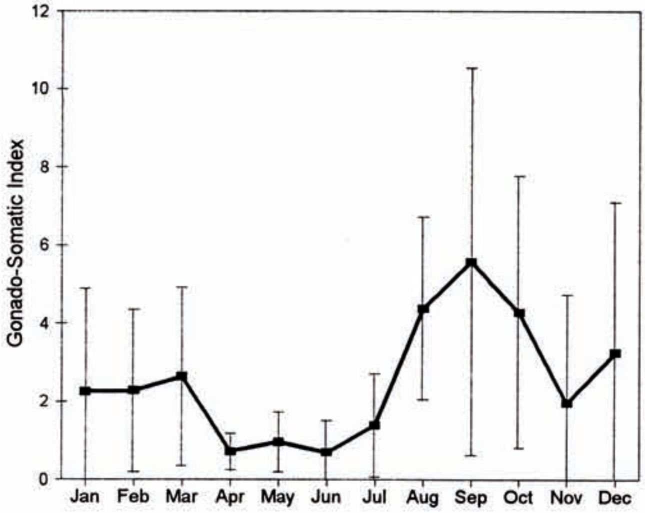


Fig. 2. - The mean monthly gonado-somatic indices for *Diplodus sargus capensis* sampled in the TNP between April 1989 and December 1990 (n = 299).

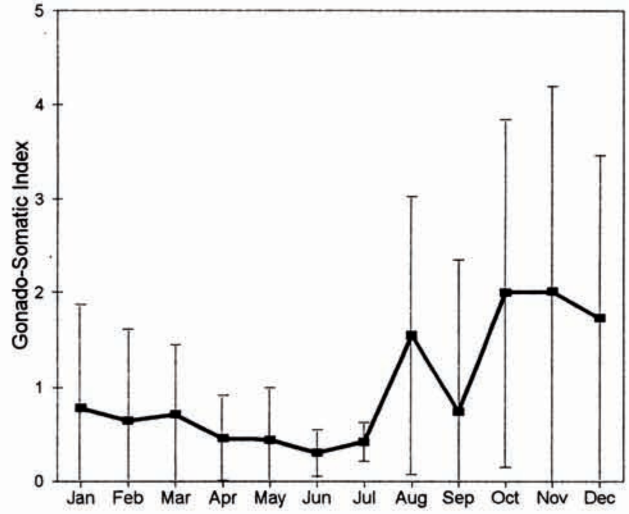


Fig. 3. - The mean monthly gonado-somatic indices for *Diplodus cervinus hottentotus* sampled in the TNP between April 1989 and December 1990 (n = 244).

1981). *D. c. hottentotus* showed a more restricted spawning season with reproductive activity extending from August through to December with a peak in October (Fig. 3). Oocyte development was similar to that of *D. s. capensis* suggesting that *D. c. hottentotus* also undergoes multiple spawnings per spawning season. The spawning season in both species was correlated with photoperiod and surface water temperature (Fig. 4). In both species, the GSI values of male fish were found to be similar to those of females, during their respective spawning seasons.

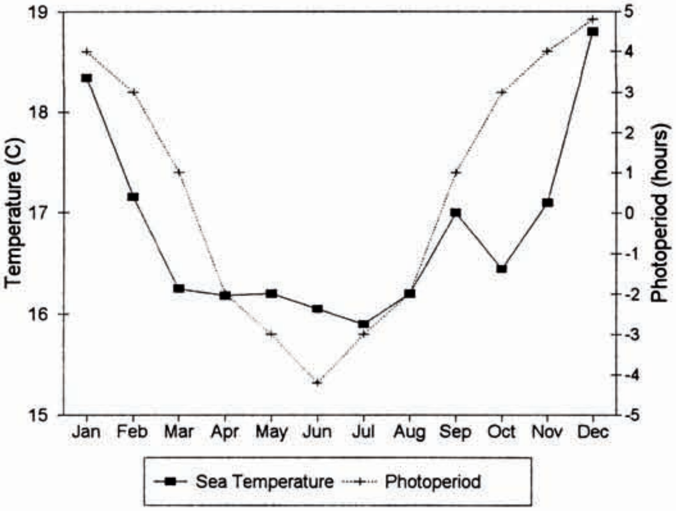


Fig. 4. - Mean monthly sea surface temperatures and photoperiod recorded in the TNP between January 1989 and December 1990.

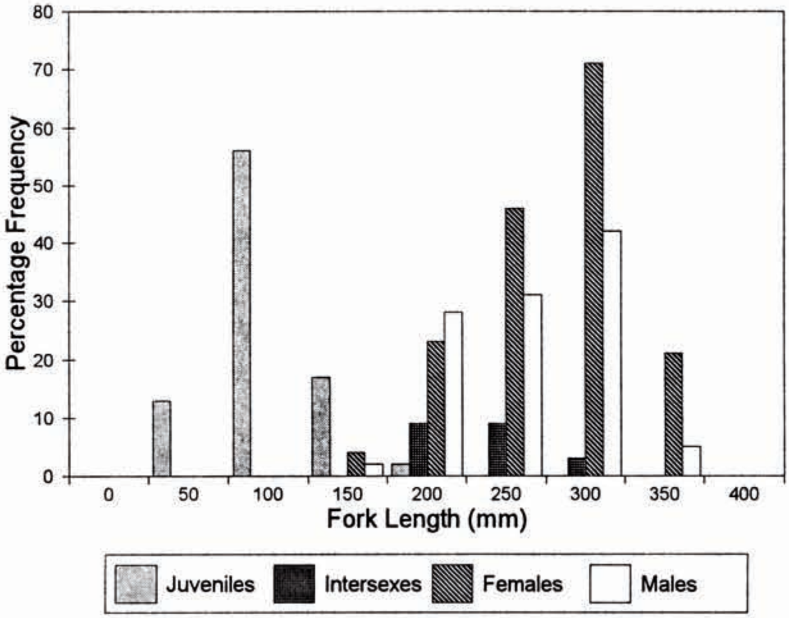


Fig. 5. - Length frequency analysis of *Diplodus sargus capensis* sampled in the TNP between April 1989 and December 1990 (n = 382).

Length frequencies, size at sexual maturity and sex ratios

Diplodus sargus capensis

A total of 382 *D. s. capensis* was sampled ranging in size from 26 mm FL (0.2 g) to 332 mm FL (1127 g). The length frequency distribution of *D. s. capensis* (Fig. 5)

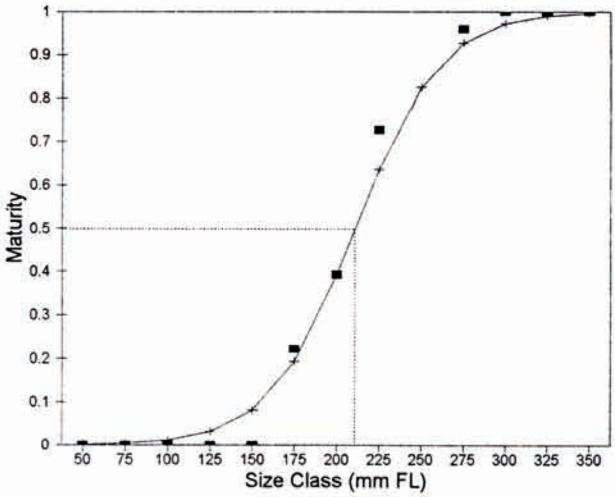


Fig. 6. - Length at 50% sexual maturity in *Diplodus sargus capensis* sampled in the TNP (n = 218).

showed that females dominated the larger size classes. Sexes were separated on a basis of macroscopic sex determination and where gonads were too small to sex macroscopically, fish were classified as juveniles. Although many fish throughout the size range showed evidence of hermaphroditism, fish were sexed macroscopically according to the dominant sexual tissue in the gonad (Bennett, 1993). Only gonads where male and female elements occurred in roughly equal proportions were termed intersexes. Intersexes were most frequently observed in the 150 to 250 mm FL size classes. Size at 50% maturity was calculated at 211 mm FL by graphing the proportion of active fish (developing, ripe or spentgonads), in each size class, during the breeding season (Fig. 6). This size at 50% maturity was equivalent to an age of three years (Mann and Buxton, 1997). To avoid any bias from the inclusion of juvenile fish which are difficult to sex macroscopically (Smale, 1988), an adult sex ratio was calculated at 1:0.1:1.98 (male:intersex:female, n = 188) using all fish greater than the size at 50% maturity. A chi-square test calculated for males and females showed that there was a significant difference from a 1:1 sex ratio ($\chi^2 = 19.78$, $P < 0.001$).

Diplodus cervinus hottentotus

A total of 304 *D. c. hottentotus* was sampled ranging in size from 41 mm FL (1.6 g) to 480 mm FL (3099 g). Male and female *D. c. hottentotus* showed similar length frequency distributions (Fig. 7). Only four intersexual gonads were observed. Size at 50% maturity was calculated at 280 mm FL (Fig. 8), which corresponds with an age of approximately six years (Mann and Buxton, 1997). An adult sex ratio was calculated at 1.23:1 (male:female, n = 105) and a chi-square test showed no significant difference from a 1:1 sex ratio ($\chi^2 = 1.15$, $P > 0.05$).

Gonadal development

The gonads of both species developed from immature ovotestes in which the testicular and ovarian elements were clearly separated by connective tissue. The ovotestis consisted of an ovarian lobe in the dorso-lateral region of the abdominal cavity, the

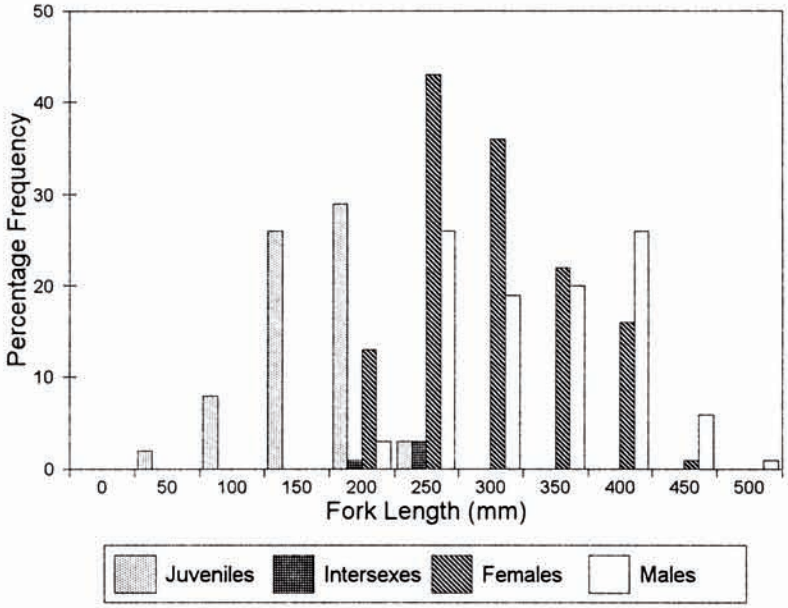


Fig. 7. - Length frequency analysis of *Diplodus cervinus hottentotus* sampled in the TNP between April 1989 and December 1990 (n = 304).

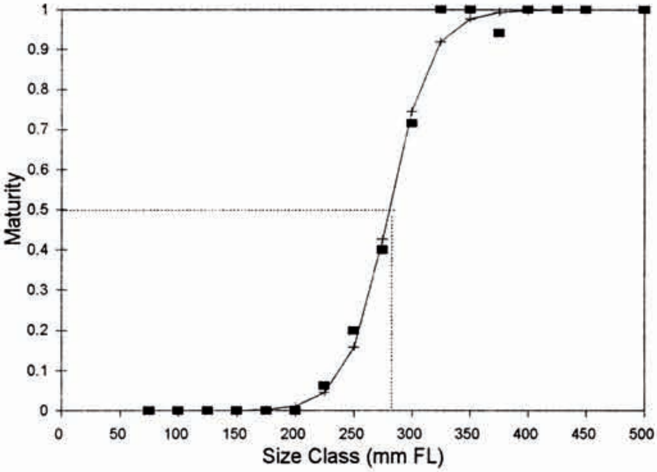


Fig. 8. - Length at 50% sexual maturity in *Diplodus cervinus hottentotus* sampled in the TNP (n = 132).

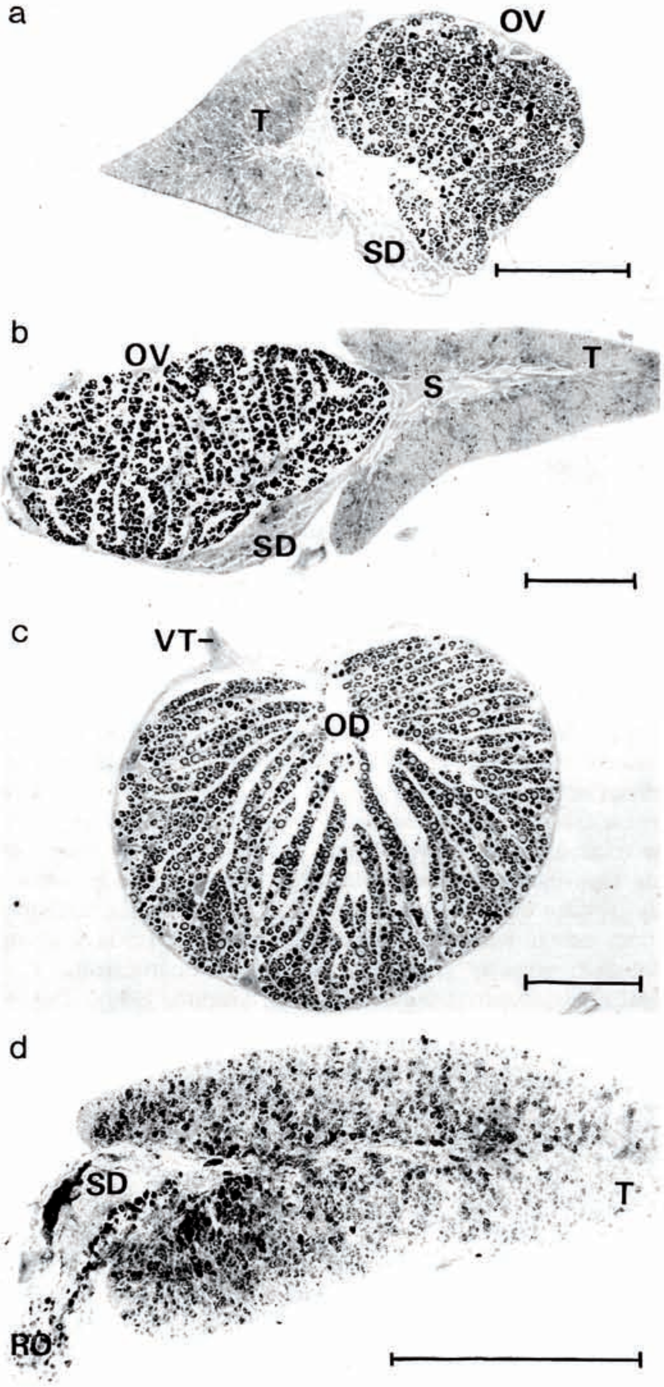
testicular lobe was ventro-lateral to the ovarian lobe. Posteriorly, the ovarian lobes fused to form a common oviduct, while folds of connective tissue formed a sperm duct that partially encircled the oviduct. This type of juvenile bisexuality is a common feature in the Sparidae (Buxton and Garratt, 1990) and is associated with the fact that teleost gonads arise from a single primordium which initially lacks male and female elements (Atz, 1964). Histological sex determination was only possible once the fish had reached approximately 100 mm FL in *D. s. capensis* and 180 mm FL in *D. c. hottentotus*. In smaller fish the gonad consisted primarily of undifferentiated gonial cells, the sex of which could not be determined. Gametogenesis in both species was similar to that described for *D. sargus* (Micale and Perdichizzi, 1994) and other sparid species (Coetzee, 1983; Buxton, 1990).

Diplodus sargus capensis

To determine the pattern of gonadal development occuring in *D. s. capensis*, gonads from 163 fish of successive size classes were described on a basis of gross-anatomical and histological observations. Gonads were classified as one of four distinguishable types. A Type I gonad consisted of a non-functional ovotestis in which testicular and ovarian elements constituted similar proportions (Fig. 9a). A Type II gonad consisted of an ovotestis in which the testicular portion was dominant and was actively undergoing spermatogenesis. The ovarian portion remained intact and was only partially enclosed by the sperm duct (Fig. 9b). Oogenesis in the ovarian portion was curtailed at the late perinuclear stage whereafter oocytes underwent atresia similar to that described for pre-vitellogenic oocytes by Yamamoto (1956). Dormant oocytes of this nature have been described in protandrous sparid species (Reinboth, 1970; Yeung and Chan, 1987), but can also be found in the ovotestes of rudimentary hermaphrodites (Coetzee, 1983; Smale, 1988). A Type III gonad consisted of a dominant ovarian portion with a lateral flap of vestigial testicular tissue (Fig. 9c). In large females, particularly during the breeding season, the testicular flap was completely atrophied and no longer visible. A Type IV gonad consisted of a dominant, functional testis which had completely enveloped the ovarian portion (Fig. 9d). The latter consisted of a rudimentary oviduct containing a band of pre-vitellogenic oocytes. In most cases this rudimentary ovarian portion was not visible macroscopically.

The sequence of development of gonadal types in successive size classes is shown in figure 10. Gonads of all fish developed from a non-functional, Type I ovotestes. In the 0-100 mm size classes no fish had yet differentiated into a discernable sex. As the fish increased in size, either the ovarian or the testicular portion of the ovotestis became dominant. The size at which one sex became dominant did not appear to be fixed, with some individuals differentiating at a small size (130 mm FL) while others retained a non-functional Type I ovotestis until shortly before sexual maturation (220 mm FL). Males developed from the Type I gonad into either a Type IV male or an intermediate Type II gonadal condition which, although containing active spermatogenic tissue, still retained an inactive ovarian portion. A Type II gonad represents a bisexual functional male that retains the potential to develop into either a unisexual functional male (Type IV) or a unisexual functional female (Type III). Females (Type III gonad) either developed directly from the juvenile ovotestis (Type I) or from a Type II gonad which changed sex into a functional female. *D. s. capensis* could therefore be considered as a digynic species having both primary and secondary females in the population (Sadovy and Shapiro, 1987; Buxton and Garratt, 1990).

Fig. 9. - Transverse sections of the four gonad types from *Diplodus sargus capensis*. **a**: Type I, 164 mm FL specimen; **b**: Type II, 203 mm FL specimen; **c**: Type III, 188 mm FL specimen; **d**: Type IV, 201 mm FL specimen. Abbreviations: OD = oviduct; OV = ovary; RO = rudimentary oviduct; S = spermatozoa; SD = sperm duct; T = testis; VT = vestigial testis. Scale bars = 1 mm.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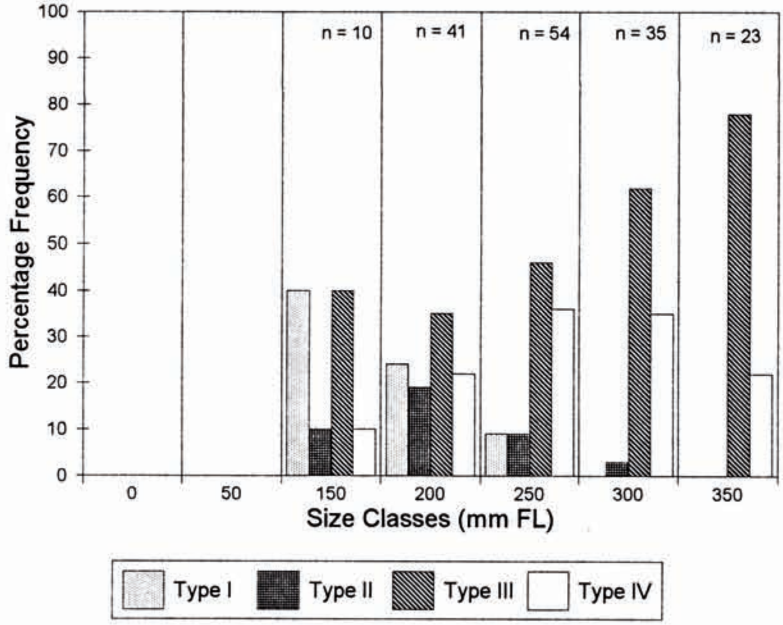

Fig. 10. - The developmental sequence of gonadal types in successive size classes of *Diplodus sargus capensis* from the TNP (n = 163).

Four examples of transitional gonads were found in fish measuring between 223 and 296 mm FL. These gonads showed evidence of degenerating testicular tissue and developing ovarian tissue (Fig. 11a). They consisted of an ovarian portion undergoing normal oogenesis with some oocytes showing secondary yolk vesicle formation and a distinct follicular layer. Although the sperm duct still contained sperm from previous spawning, the testicular tissue showed definite signs of degeneration with spermatogonia being actively phagocytosed by leucocytes (Fig. 11b). The occurrence of these transitional gonads provided evidence that some fish in the population undergo a facultative sex change from male to female. The potential of a Type II gonad to change sex into a functional female is probably dependent on social or environmental cues rather than being genetically predetermined (Reinboth, 1988; Shapiro, 1989). This would explain the variation in size of fish at sex change.

Diplodus cervinus hottentotus

The structure of the juvenile ovotestis in *D. c. hottentotus* was similar to that described for *D. s. capensis*. Differentiation of the dominant sex took place well before sexual maturation. In developing males, the ovarian portion degenerated until only a rudimentary oviduct, sometimes surrounded by a band of pre-vitellogenic oocytes, was still visible. The rudimentary oviduct was almost completely enveloped by the testis and developing sperm duct (Fig. 12a). The testicular tissue in differentiating males consisted predominantly of spermatogonia, with a few isolated clumps of primary spermatocytes. In developing females the ovarian element became dominant while the testis was reduced to a thin, lateral flap of tissue (Fig. 12b). Of the 304 fish sampled only four intersexual gonads were recognised macroscopically. Histological examination of these ovotestes

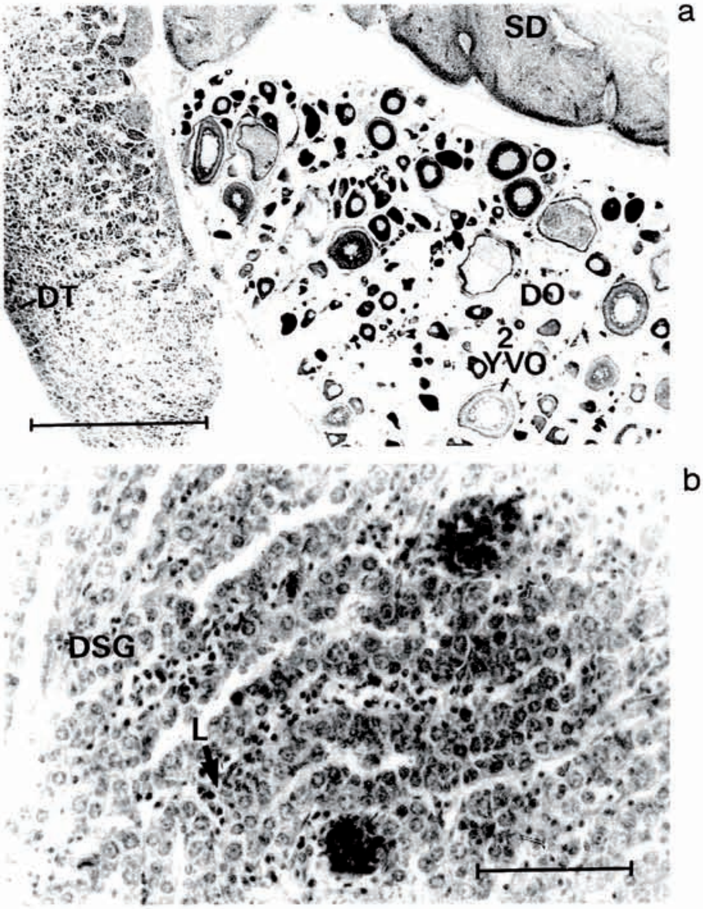

Fig. 11. - *Diplodus sargus capensis* (297 mm FL). **a**: Section of a transitional gonad changing sex from male to female, scale bar = 0.5 mm; **b**: Section of degenerating testicular tissue from the same specimen viewed under high magnification. Abbreviations: DO = developing ovary; DSG = degenerating spermatogonia; DT = degenerating testis; L = leucocytes; SD = sperm duct (containing sperm); 2°YVO = secondary yolk vesicle oocyte. Scale bar = 200 µm.

showed that they consisted of immature developing testes and a dormant ovarian portion which was probably representative of the retention of a non-functional, juvenile ovotestis. This type of development, where either the testis or the ovary matures after a stage of juvenile bisexuality, is typical of rudimentary hermaphrodites (Buxton and Garratt, 1990) which mature as functional gonochorists.

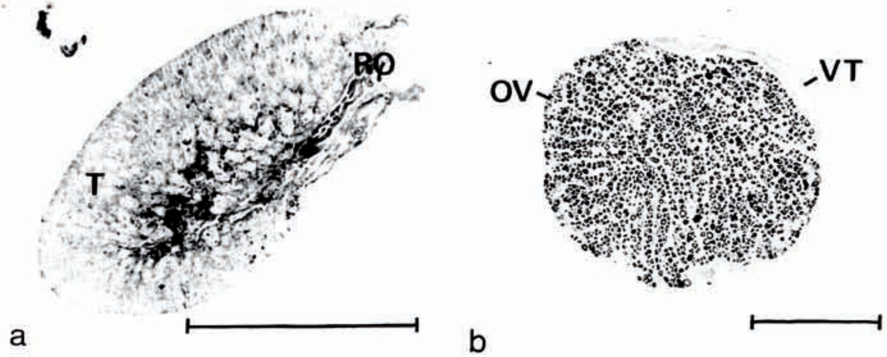

Fig. 12. - **a**: Section of a developing testis from *Diplodus cervinus hottentotus* (188 mm FL); **b**: Section of a developing ovary from *D. c. hottentotus* (197 mm FL). Abbreviations: OD = oviduct; RO = rudimentary oviduct; T = testis; VT = vestigial testis. Scale bars = 1 mm.

DISCUSSION

Reproductive seasonality

In *D. s. capensis* and *D. c. hottentotus* the gonado-somatic indices showed that both species spawned during spring and summer, similar to many other South African sparid species. The spawning seasons of both *Diplodus* species correlated well with the observed summer peak in abundance of their eggs off the south-western Cape coast (Brownell, 1979). The extended spawning season of *D. s. capensis* (August to March) and the ability of individuals to spawn repeatedly ensures that the risk of catastrophic mortality of eggs and planktonic larvae is reduced (Thresher, 1984). This spawning strategy also ensures that recruitment of juveniles into inshore nursery habitats is spread over a period of time, thereby minimizing the possibility of inter and intraspecific competition for food and habitat space (Sale, 1974; Johannes, 1978; Christensen, 1978). The more restricted spawning season of *D. c. hottentotus* (August to December) was similar to that of a number of other sympatric sparid species including *Chrysoblephus laticeps*, *C. cristiceps* (Buxton, 1990) and *Sparodon durbanensis* (Buxton and Clarke, 1991). It appears that reproduction in all of these species is geared to take advantage of the beneficial conditions (temperature, food availability, etc.) occurring during this time of year in order to ensure greatest survival of young.

This study showed that gonad maturation in both species was correlated with increasing photoperiod and water temperature during July and August. Photoperiod is commonly temperature sensitive (de Vlaming, 1972) and it is generally accepted that most fish species have a range of temperatures within which spawning can take place (Lagler *et al.*, 1962). Inshore water temperatures along the south-eastern Cape coast show considerable fluctuation during the summer months due to frequent upwelling events (Schumann *et al.*, 1982). It is therefore probable that spawning, in both species, occurs when optimum, stable temperatures prevail after westerly winds cause a downwelling process and warmer water moves close inshore (Schumann *et al.*, 1982).

It has been recognised that fish from tropical areas generally start spawning before those from more temperate areas (Coetzee, 1983). In KwaZulu-Natal *D. s. capensis* spawn between May and November (Joubert, 1981), while in the Eastern Cape spawning occurs between June and December (Lasiak, 1983; Beckley, 1985; Coetzee, 1986). This study showed that *D. s. capensis* in the TNP (south-eastern Cape) spawn between August and March with a peak recorded during spring. Bennett (1989) recorded an influx of small juvenile *D. s. capensis* (< 25 mm TL) into the surf zone in False Bay (southern Cape) between January and August. Daily increment analysis (Lang and Buxton, 1993), has shown that larval *D. s. capensis* take two to three months to become juveniles of the size recorded by Bennett (1989), which suggests that spawning in this region occurred during late summer. This evidence suggests that spawning in *D. s. capensis*, which occurs from southern Mozambique to Angola (Smith and Heemstra, 1986), is strongly influenced by water temperature with spawning occuring during winter and spring in subtropical KwaZulu-Natal waters and during spring and summer in the more temperate Cape waters. Correlation between months of peak spawning in *D. s. capensis* and mean monthly temperatures recorded along the South African coast (Bang and Pearce, 1978; Shannon, 1989; Hanekom *et al.*, 1989) indicates that optimum spawning temperatures range from approximately 17 to 20°C.

No attempt was made to estimate the fecundity of either species due to the problems associated with counting eggs of multiple spawners (Bagenal and Braum, 1968; Garratt, 1985). However, judging from the small size of mature eggs (< 1 mm in diameter) and the high GSI values recorded in ripe females (up to 25% of body weight), both species have relatively high fecundities, especially *D. s. capensis* where particularly high GSI values were noted.

Population structure

Diplodus sargus capensis

Bimodal size frequencies with males occupying the smaller size classes and male biased sex ratios have often been used as diagnostic criteria for the occurrence of protandrous sex change in fishes (Sadovy and Shapiro, 1987; Yeung and Chan, 1987). The length frequency distribution of *D. s. capensis* showed that there was no clear separation in modal size between males and females, although females dominated the larger size classes. This was evident in an adult sex ratio significantly biased by females. Futhermore, the occurrence of primary females in the population suggested that *D. s. capensis* was not a protandrous hermaphrodite under the classical definition.

Histological examination of gonadal development showed that *D. s. capensis* is a digynic species. Males and females both mature from a non-functional intersexual phase but some males retain the capability to change sex into secondary females. In order for this interpretation to be consistent with a definitive diagnosis of protandrous sex change and not to be confused with a prolonged juvenile bisexual phase (Sadovy and Shapiro, 1987; Matsuyama *et al.*, 1988), individuals must first be shown to have functioned as males before changing sex to female (Buxton and Garratt, 1990). Mere evidence of sperm maturation occurring in the testicular region of an ovotestis is not sufficient to infer male functionality (Buxton and Clarke, 1991). The occurrence of Type II gonads in fish larger than the size at 50% sexual maturity (> 211 mm FL), which possessed a functional sperm duct containing sperm during the spawning season, provided strong evidence that these fish were in fact functional males. Histological evidence of transitional Type II gonads was, therefore, suggestive of protandric development amongst certain individuals in the population.

Work done on captive *D. sargus sargus* from the Mediterranean has shown that the majority of fish mature first as males with sex change occurring at different ages (Micale *et al.*, 1987; Micale and Perdichizzi, 1994). The occurrence of a few individuals that mature as females has led to the usage of the term "unbalanced" hermaphroditism which is characterised by great variability in sexual phenotype (Micale *et al.*, 1987). Similarly Abou-Seedo *et al.* (1990) found that protandrous sex change took place in the majority of *D. sargus kotschyi* from Kuwait Bay during their second year of life but they also found that a number of fish in the population differentiated and functioned only as females. Although there is a lack of clarity in the terminology used, coupled in some instances with superficial macroscopic observation, digyny does appear to be a common reproductive style in the various subspecies of *D. sargus*. Similar plasticity in the expression of the sexual phenotype has been described in other sparid species such as *Acanthopagrus australis* (Pollock, 1985) where some females in the population are derived from protandric males while others differentiate straight from the bisexual juvenile condition. The assumption that sex change in fishes is genetically predetermined (Ghiselin, 1969), is therefore, not sufficient to explain its intermittant occurrence amongst these species.

Diplodus cervinus hottentotus

Similar size ranges for males and females and a sex ratio that does not differ significantly from unity are distinctive features of gonochoristic species (Buxton and Garratt, 1990). Histological examination of gonadal development in *D. c. hottentotus* confirmed that this species is a rudimentary hermaphrodite where males and females develop from an immature bisexual gonad prior to sexual maturation. No evidence of sex change was found in mature individuals. Buxton and Garratt (1990) also refer to this group as "late" gonochorists to distinguish them from "true" gonochorists in which hermaphroditic tissue is not found. They suggest that all sparids previously classified as "true" gonochorists should in fact be re-classified as rudimentary hermaphrodites owing to the occurrence of male and female elements in the early sparid gonad. Rudimentary hermaphroditism appears to be a common reproductive style amongst southern African sparids and has been reported in a number of species including *Polysteganus undulosus* (Ahrens, 1964), *Cheimerius nufar* (Coetzee, 1983; Garratt, 1985), *Petrus rupestris* (Smale, 1988), *Sparodon durbanensis* (Buxton and Clarke, 1991) and *Pachymetopon grande* (Buxton and Clarke, 1992).

Spawning behaviour

Diplodus sargus capensis

Evidence suggests that sex change in fish is initiated primarily by behavioural or demographic alterations within a fish's social system (Shapiro, 1989). Of these alterations, the type of mating system employed appears to exert a major influence (Warner, 1988). No spawning behaviour was observed in *D. s. capensis*, however, various morphological and indirect behavioural characteristics were used to speculate on the type of mating system used. The most important of these characteristics included the similar size of functional males and females (monomorphism) and the large testis size in functional males. Similarity in the size of functional sexes suggests that reproductive success is not size related (Warner, 1984; Buxton and Garratt, 1990). Large testis size is seen as an advantage in terms of sperm competition where males compete with each other to fertilize eggs (Buxton and Garratt, 1990). From these observations Buxton and Garratt (*op. cit.*)

suggest that mating should take place in random pairs matched by size or in a group spawning sequence.

It is therefore possible that *D. s. capensis* adopt a similar group spawning behaviour to that described for *Acanthopagrus berda* (Garratt, 1993). In a situation where males congregate to attract females (male dominance polygyny) (Emlen and Oring, 1977), male-male competition is strong (many Type IV males) and selective pressure may be placed on Type II males to change sex to female. However, if there are few Type IV males present, selective pressure for Type II males to change sex is reduced.

Diplodus cervinus hottentotus

Large shoals of *D. c. hottentotus* (up to 30 fish) were observed on rare occasions during the spawning season and it is suggested that mating in this species also takes place in a group spawning sequence. Monomorphism and large testis size in this species provides further evidence in support of group spawning behaviour (Buxton and Garratt, 1990). In group spawners the potential for polygamy would be reduced and little sexual selection would occur. Monomorphism and a sex ratio close to unity as found in *D. c. hottentotus* would therefore be expected (Buxton and Clarke, 1991). This type of spawning behaviour has been postulated in other sparid species which are rudimentary hermaphrodites (Smale, 1988; Buxton and Clarke, 1991; 1992).

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